ON THE CUTICLES OF SOME INDIAN CONIFERS

RUTH HOLDEN

(WITH PLATE XI)

In no branch of science has the improved technic of the last few decades brought about a greater increase of knowledge than in paleobotany. The old purely systematic work based on impressions alone has been supplanted, or at least supplemented, by a microscopic examination of structurally preserved material. The results have been valuable along both geological and botanical lines; the former by insuring the reliability of stratigraphical correlations through more accurate diagnoses, and the latter by indicating the relationships between living groups of plants through more extensive information regarding their extinct ancestors. Recently the examination of epidermal tissues has opened up a new line of attack. This method has been especially fruitful among the Cycadales, and our ideas of the affinities of fossil cycads have been materially altered. The next group to be attacked is obviously the Coniferales. Such genera as include both fertile and sterile shoots have, as a rule, certain definite diagnostic characters, but where a knowledge of the reproductive parts is lacking, chaos reigns supreme. In a few cases structurally preserved material has been examined, and the results have shown in a very striking manner the futility of attempting to classify according to impressions alone, and the folly of affiliating specimens with the living genera which they may simulate in external appearance. When we consider that *Thuyitis cretacea* and *Widdringtonitis Reichii*, both formerly included in the Cupressineae, have been proved to be araucarians (14), the truth of this statement is evident. In cases where the state of preservation precludes the possibility of a satisfactory investigation of the internal anatomy, the next best thing is to examine their cuticles. Such work has been undertaken in a few instances, as for example, ZEILLER (31) and BERRY (3) on *Frenelopsis*, SCHENK (21) and NATHORST (19) on *Palissya*, THOMPSON (30) on *Frenelopsis*, *Androvettia*, and

Brachyphyllum, and THOMAS (**28**) on *Taxites*. In addition to these, there are many scattered references to the distribution of stomata in the description of coniferous leaves, as by JEFFREY (**14**), BERRY (**3**), STOPES (**26**), and STOPES and KERSHAW (**27**), but too often there has been no attempt at correlation with living forms.

In the structure of the epidermis there are certain features which are constant, and certain others which seem to vary, not only within the genus or species, but even in different individuals. For example, in the case of flattened dorsiventral leaves of the *Taxites* type, the stomata are always abundant on the lower surface, but may or may not be present on the upper as well. Thus MALHERT (**16**) states that in *Sequoia sempervirens*, *Abies*, and *Pseudotsuga* they are present on both surfaces, but I have found many instances where they were completely lacking above. As regards numbers, such a character must obviously vary, and even a hasty examination shows flaws in the elaborate keys of BERTRAND (**6**), where *Araucaria excelsa* is described as having 3 nerves, and 4 groups of stomata of 5 rows each; *A. Balansae*, with 5 nerves, and 4 groups of stomata of 8 rows each, etc. This is commented on by SEWARD and FORD (**25**): "The veins vary in number in the leaves of a species according to the part of the lamina examined and the age of the leaf. The rows of stomata exhibit similar varieties; for example, *Araucaria imbricata*, said by BERTRAND to have 70 rows, may have any number from 60 to 80."

As regards arrangement of the stomata with reference to each other, there seems to be remarkable constancy. Thus in practically all leaves of the *Taxites* type, they are in regular rows on each side of the midrib, with the long axis of the stoma parallel with the edge of the leaf. This seems to hold irrespective of the family to which the specimens belong: *Pseudotsuga*, *Tsuga*, *Abies*, and *Keteleeria* in the Abietineae; *Widdringtonia* in the Cupressineae; *Cunninghamia* and *Sequoia sempervirens* in the Taxodineae; *Taxus*, *Cephalotaxus*, and *Torreya* in the Taxineae; and *Prumnopitys* and *Saxegothea* in the Podocarpineae.

The character of the epidermal cells has not been fully described by most investigators, but there is every reason to regard it as

fixed. Such is undoubtedly the case with cycads; for example, *Ptillophyllum hirsutum* (**29**) from Marske is identical both with specimens from Whitby in the Sedgwick Museum, Cambridge, England, and with others collected by the writer from Navidale, Sutherland, Scotland. Since there is such specific constancy in the cycads, it is probable that the same holds true for the conifers, although too little work has been done on the latter to speak dogmatically.

On the other hand, so far as uniformity within large groups is concerned, there seems to be less in the case of the conifers than in the cycads. To illustrate: the Bennettitales group may be marked off from the Nillsoniales by the sinuous-walled epidermal cells of the former as contrasted with the straight walls of the latter; while within the Abietineae, sinuous walls have been observed only in some species of *Abies* and *Keteleeria;* in the Taxodineae, only *Cunninghamia;* in the Podocarpineae, *Saxegothea* and *Podocarpus;* and in the Araucarineae, *Araucaria*. Furthermore, this tendency toward diversity even within a single genus is much more marked among the conifers than among the cycads. Thus, *Dictyozamites Johnstrupi* Nath. (**18**) from Bornholm is substantially like *D. Hawelli* Seward (**23**) from Marske, and the three species of *Ptillophyllum* (*P. hirsutum* from Yorkshire and Sutherland, *P. pecten* from Yorkshire, and *P. acutifolium* from India) are very similar, both in the sinuous walls and in arrangement of stomata. Within the genus *Araucaria*, on the other hand, members of § COLYMBEA have the long axis of all the stomata parallel to the leaf margin, while in § EUTACTA there is no uniform angle; or even in § EUTACTA, *A. Cunninghami* has distinctly sinuous-walled epidermal cells, while in *A. Cookii* and *A. elegans* they are straight. A similar state of affairs exists for the genus *Podocarpus*, where within § EUPODOCARPUS, *P. macrophylla* and *P. totara* have sinuous walls, whereas in *P. alpina* and *P. elatus* they are straight.

Another feature which seems to be fairly constant is the presence of characteristic thickenings of the cuticle, either on the accessory cells of the stomata or on those of the general epidermis. These may constitute teeth projecting into the cavity of the stomatal opening,

as in *Frenelopsis* (30), or they may make a rim around the opening itself, as in species of *Taxus*, *Juniperus*, *Thuja*, *Libocedrus*, etc. In other cases, all the epidermal cells, at least in the vicinity of the stomata, may have peculiar knoblike projections of cuticle. These last seem to be diagnostic in their constancy; they are present in *Taxus baccata*, including vars. *erecta*, *fastigiata*, and *variegata*.

As a last feature, we may refer to the shape and extent of the lignified lamellae of the guard cells. These have been found to be absolutely constant in the case of the cycads, and the investigations of the writer on the conifers indicate a considerable uniformity not only within the species, but even within the genus or family. Thus in all the members of the Araucarineae examined, the ventral thickenings are relatively larger and overlap the dorsal to a greater extent than in any other family. Unfortunately, however, the employment of this feature in examining fossil conifers is usually rendered impossible through imperfect preservation, although it has been found to be of considerable value for the cycads.

From this discussion of the significant points in structure of the epidermis, two conclusions may be drawn. The first is that the number and general distribution of stomata (upper or lower surface of leaf) is variable within the species, but that the character of the walls of the epidermal cells (uniformity of thickness, cuticular projections, straight or sinuous), arrangement of stomata (whether or not in rows, angle of long axis with reference to leaf margin), and extent of lignified lamellae of guard cells, are remarkably constant. The second relates to the phylogenetic value of these features and seems to indicate that it is small. For example, all leaves of the *Taxites* type, no matter to what family they belong, have long rows of stomata on each side of the midrib of the under surface of the leaf all with their long axes parallel to the margin. Similarly, leaves of the *Thuyites* type, as exemplified by *Dacrydium*, *Arthrotaxis*, *Tetraclinus*, *Thuya*, *Juniperus*, *Cupressus*, *Libocedrus*, etc., have the stomata scattered indiscriminately, usually avoiding the midrib, but with no sign of rows or constant angle. It seems obvious, accordingly, that the investigation of cuticles is of importance to the systematic botanist engaged in accurate specific diag-

noses, but that it is of little interest to one concerned with the broader problem of the evolutionary history of the Coniferales.

Palissya

Among the numerous specimens of the genus *Palissya* sent by the Director of the Indian Geological Survey to Professor SEWARD, there were but two with cuticle preserved. One of these, from the Umia group of Thrombow, is labeled *Palissya* sp.; the other, from the Jabalpur group, is called *P. indica*, Fstm., both being Jurassic. OLDHAM and MORRIS had previously described specimens of this character as *Taxitis indicus*, but FEISTMANTEL transferred them to the genus *Palissya* Endl., believing them to be very near to the European *P. Brauni* (9). The two specimens differ but slightly in external appearance, and the structure of the cuticle indicates that they are specifically identical. The general habit is shown in fig. 1, and it is evident that in the spirally arranged, linear, and decurrent leaves, they resemble closely typical specimens of *Taxitis* or *Palissya*. The only discrepancy is the absence of a midrib, a feature noticed also by FEISTMANTEL. A general view of the epidermis is given in fig. 9. Toward the left are represented the cells of the upper surface, angular in shape, with straight walls and no stomata; toward the right, those of the lower, showing the stomata scattered with no semblance of regularity, but with their long axes more or less parallel to the margin of the leaf (see also fig. 11). Details of a single stoma are shown in fig. 4. The accessory cells are usually 6 in number, though not rarely 4 or 5; the guard cells are deeply sunken and often lacking; occasionally, however, the thickenings persist. Sometimes, as in fig. 4, the dorsal lamellae remain, while the ventral at one or both ends disappear. Not infrequently there are a few stomata on the upper surfaces of the leaf, and on the stem itself there are usually a few, due probably to the decurrent nature of the leaf bases. In no case, however, is there the slightest indication of the central astomatic region which would normally cover a midrib. The fact that the midrib is indistinguishable either in gross specimens or in detached cuticles, suggests a doubt as to the propriety of referring these specimens to either *Taxitis* or *Palissya*. The former is always

described as "uninerva" (see SCHIMPER **22,** UNGER **32,** etc.), and THOMAS (**28**) has pointed out that the stomata, at least in *Taxitis zamioides*, occur in two bands, one on either side of the midrib. *Palissya* is also "uninerva" in Endlicher's original description; and in *P. sphenolepsis* (**19**) and *P. Brauni* (**21**), the stomata have the same distribution as in *Taxitis*. It seems clear, accordingly, that these Indian specimens do not conform to the *Taxitis* type, as represented either by the living *Tsuga*, *Abies*, *Taxus*, etc., or by the fossil *Taxitis* or *Palissya*. Among other existent forms the absence of parallel veins separates them from the Araucarineae and from the genus *Podocarpus*. A possible affiliation would be with *Dacrydium* or *Arthrotaxis*, but in both these genera, although there is no obvious midrib in gross specimens, preparations of the cuticle show a marked astomatic path running down the center of the lower surface of the leaf. By the process of elimination, we are driven to the only other flat-leaved conifers, namely Cupressineae of the *Retinospora* type, such as are found in seedlings of *Thuya* or *Juniperus*. Here, also, the stomata are scattered irregularly, sometimes on the upper surface, sometimes on the lower, sometimes avoiding the midrib, but often disregarding its presence; furthermore, the leaves are not constricted at the base, and they are markedly decurrent. The only objection to referring them to that family is the spiral phyllotaxis, but when the diversity existing in nearly related forms, both living and fossil, is considered, it seems doubtful whether this point is of much importance. For example, the leaves of *Podocarpus* are spiral except § NAGEIA, where they are decussately opposite; again, in all the Araucarineae they are spiral except in the two fossil forms *Thuyites cretacea* and *Androvettia* (**14**). The different types of phyllotaxis sometimes found in the same specimen add further evidence in the same direction. Thus, the *Retinospora*-like seedling leaves of *Thuya* and *Juniperus* are occasionally arranged in a spiral fashion, which soon gives way to characteristic verticils. DAGUILLON (**7**) has described an *Abies* seedling with whorled instead of spiral leaves, and MASTERS (**17**) one of *Cephalotaxus* with first a pair of opposite leaves and then a whorl of four. Moreover, although the foliage leaves of *Microcachrys* are decussately opposite, the sporophylls, both microsporangiate and megasporangiate, are in spirals.

From these considerations it seems evident that this so-called *Palissya* presents a type of leaf new to paleobotany, and to indicate its similarity to living forms, it may advantageously be called **Retinosporitis indica.** It should be emphasized, however, that this name is not intended to signify that it is necessarily closely related to *Retinospora*, or indeed that it belongs to the Cupressineae at all; but merely that in external appearance and epidermal structures it has certain features in common with that genus.

Echinostrobus expansus

The next specimen to be described has been referred by FEISTMANTEL (8) to *Echinostrobus expansus*, with the statement that it is identical with *Thuyitis expansus* L. & H. (15). Fig. 2 shows the general decussately opposite disposition of the leaves; other figures are given by FEISTMANTEL (*loc. cit. pl. 9010);* and fig. 6 shows the epidermis of a single detached leaflet. The dark crescent in the upper part may correspond to what was originally the free end of the leaf. Above it is a rim of fairly regularly arranged cells which is probably the "marginal depression" mentioned by LINDLEY and HUTTON, while the astomatic part to the left may have been overlapped by the leaf adjacent to it. The epidermal cells are exceedingly irregular in shape, though below the midrib they tend to become somewhat elongated. The stomata are scattered without definite order beyond the fact that there is an astomatic area down the center, and that they are more abundant near the margins, where they might have been partially shaded by the adjacent leaves. The accessory cells (fig. 5) are almost invariably 4 in number, beneath them is at least one intercalary layer, and then the guard cells, which have practically disappeared. The depth to which the stomata are sunk is probably correlated with their relative abundance and direct exposure to the sun's rays, for in living conifers of similar habit they are often less deeply sunken, but are usually confined either to the under surface of dorsiventrally flattened shoots (for example, *Thujopsis dolabrata*), or to the depressions where one leaf overlaps another (for example, *Libocedrus decurrens*, *Thuja gigantea*, *Frenella* sp., etc.).

The sytematic position of branches of this type has long been a disputed point. They were first referred by LINDLEY and

HUTTON (15) to *Thuyitis* because of the verticillate arrangement of the leaves. SCHIMPER (22) then transferred them to STERNBERG'S taxodineous genus *Echinostrobus*, where the leaves are sometimes spiral and sometimes whorled. SAPORTA (20), however, pointed out the inadvisability of this step and put them back into the Cupressineae, this time as *Palaeocyparis expansa*. SEWARD (24) refers to the difficulty of distinguishing between the whorled leaves of *Thuyitis* and the spiral ones of *Brachyphyllum*, and suggests (23) that, at least so far as the specimens of LINDLEY and HUTTON are concerned, the two genera are identical. The structure of the cuticle is not without bearing on this question, for in the species of the latter which have been examined—*B. macrocarpum* NEWBURY (14), *B. Münsteri*, and *B. affine* (21)—the stomata are in long rows alternating with strands of sclerenchyma. This condition, of course, is entirely different from that of *Thuyitis expansus*, though it is singularly like *T. Schlonbachi* SCHENK (21) and the living podocarpineous genus *Microcachrys*. For a parallel, we are driven to the Taxodineae (*Arthrotaxis*) or the Cupressineae (*Thuja*, etc.), and though, as suggested above in the case of *Palissya*, phyllotaxy is not an invariable test for affinities, still in view of the fact that, as a whole, the leaves of the Taxodineae are in spirals and those of the Cupressineae in whorls, it would seem to be advisable to retain the original name, and, at least until an examination of their internal structure settles the question of affinities, to continue to call shoots of this type *Thuyitis expansus*.

Taxitis tenerrimus

The next specimen to be described has been referred by FEISTMANTEL (10) to *Taxitis tenerrimus*, and the spiral arrangement of the linear, uninerved, and decurrent leaves, shown in fig. 3, indicates the correctness of this identification. The cuticle of the upper surface is entirely devoid of stomata; that of the lower is represented in fig. 8. The epidermal cells are irregular in shape, with a slight tendency to become elongated below the midrib. The stomata are scattered without definite arrangement, but the indifferent state of preservation prevents any detailed description. In general, however, there are 4–6 accessory cells, and the opening

is parallel to the leaf margin. This distribution is quite unlike that of *Taxitis zamioides* (**28**), where there are two narrow rows of stomata, one each side of the midrib, and warrants at least a specific distinction. As to its affinities, it is impossible to go farther than to state that it is totally unlike *Taxus* or any other living member of the Taxineae.

Podozamites lanceolatus

The last specimen to be described was referred by FEISTMANTEL to *Podozamites lanceolatus* (**11**). Isolated leaves were found fairly commonly in the Jabalpur group of South Rewah (Jurassic), but there were none attached to the rachis. Various specimens showing the characteristic shape are represented in *figs. 2–5. pl. 1* (*loc. cit.*), and their resemblance to the type specimen of LINDLEY and HUTTON is obvious. There is no difference between the epidermis of the upper and lower surfaces; these cells (fig. 10) are all straight-walled, more or less elongated over the veins, while the stomata are confined to the area between the veins, with their long axes parallel to the margin of the leaf. The structure of a single stoma is shown in fig. 7. There are usually 6 accessory cells, rarely 4 or 5. The character of the guard cells is unfortunately difficult to determine, but there seems to be a double rim of cuticle around the opening. This appearance is constant in the best preserved specimens, but its interpretation is doubtful. Probably there was at least one row of cells intercalated between the accessory cells and the guard cells, and the rims referred to may represent cuticular projections on these intercalary cells, such as are characteristic of certain living conifers and cycads. The lignified lamellae of the guard cells have invariably disappeared.

The resemblance of the cuticle of this Indian specimen to that of *Zamites distans* Prestl., as described by SCHENK (**21**), is very close; both have straight-walled epidermal cells with stomata between the veins. In the latter, however, there are no stomata on the upper surface. The difference between *Podozamites* and *Zamites* is rather obscure, BRONGNIART including the former as a subsection of the latter. The cuticles, however, show them to be entirely distinct, for *Zamites* (**29**) has all the bennettitalean characters, sinuous-walled cells and long axis of stomata at right angles to

leaf margin; while if the affinities of *Podozamites* are cycadean at all, they are with the Nillsoniales. It seems entirely probable, however, that they are coniferous. SEWARD (**23**) has stated the pros and cons of the situation, and in view of the spiral phyllotaxis and bud scales at the base of the petiole reaches that conclusion. SCHENK (**21**), on the other hand, compares these scales to those found in the living *Cycas*, and argues that *Podozamites* cannot be related to the conifers as exemplified by *Dammara orientalis* for three reasons: (1) the leaves are not opposite; (2) the vascular tissue in the petiole is not like that of *Dammara;* and (3) the epidermal structure is different. The first reason may hold for *Zamites distans* and *Dammara orientalis*, but it does not hold for *Zamites lanceolatus*, for the original description of this species by LINDLEY and HUTTON (**15**) states that the pinnae are "sometimes opposite and sometimes alternate"; nor does it hold for other species of *Dammara*, where the leaves are spiral. The second reason seems equally questionable, for of the two vascular strands figured by SCHENK, one shows protoxylem rings and the other has the crowded hexagonal pitting characteristic of both cycads and araucarians. As regards the third reason, the difference in epidermal structure is slight; in both *Podozamites* and *Dammara* the stomata are in rows between the veins, but in the former the long axis is parallel to the edge of the leaf, while in the latter it is at right angles. The resemblance to *Araucaria* § COLYMBEA, however, seems to be very close. The phyllotaxis is the same, and both have rows of stomata with their long axes parallel to the leaf margin. Another possibility is presented by § NAGEIA of the genus *Podocarpus*. It is not suggested that *Podozamites* can be identified specifically with any living conifer; for example, the sinuous walls of *P. Nageia* and *A. brasiliana* bar them out, as do the heavily pitted epidermal cells of *A. imbricata* and *A. Bidwillii;* but it does seem fairly clear that *Podozamites* is nearer to the conifers than to the cycads.

Summary and conclusions

1. A comparative study of living and fossil conifers indicates that epidermal structures are of great value for accurate specific diagnoses, but of relatively little importance for indicating affinities.

2. On account of the character of its cuticle, the so-called *Palissya indica* of FEISTMANTEL cannot properly be referred to that or any other fossil genus; and to point out its resemblance to the living *Retinospora*, it is suggested that it be called *Retinosporitis indica*.

3. *Echinostrobus expansus* closely resembles many living members of the Cupressineae, both in epidermis and in phyllotaxy; accordingly it would seem better to retain the old name of LINDLEY and HUTTON, *Thuyitis expansus*.

4. *Taxitis tenerrimus* has a type of cuticle common to many extant conifers, and its affinities cannot be decided.

5. The epidermal structure of *Podozamites lanceolatus* constitutes another reason for referring that genus to the conifers rather than to the cycads.

In conclusion, I wish to thank Professor SEWARD for this opportunity to study the fossil conifers sent by the Director of the Indian Geological Survey, and to compare them with the living ones in the collections at the Botany School, and for valuable suggestions in regard to this work.

BOTANY SCHOOL
CAMBRIDGE, ENGLAND

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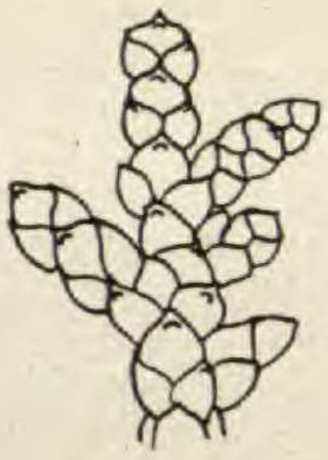

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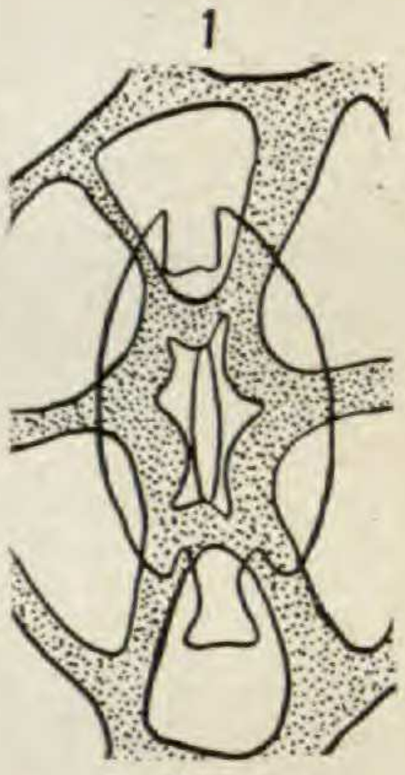

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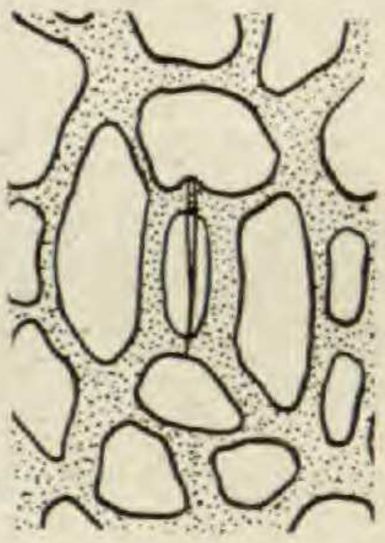

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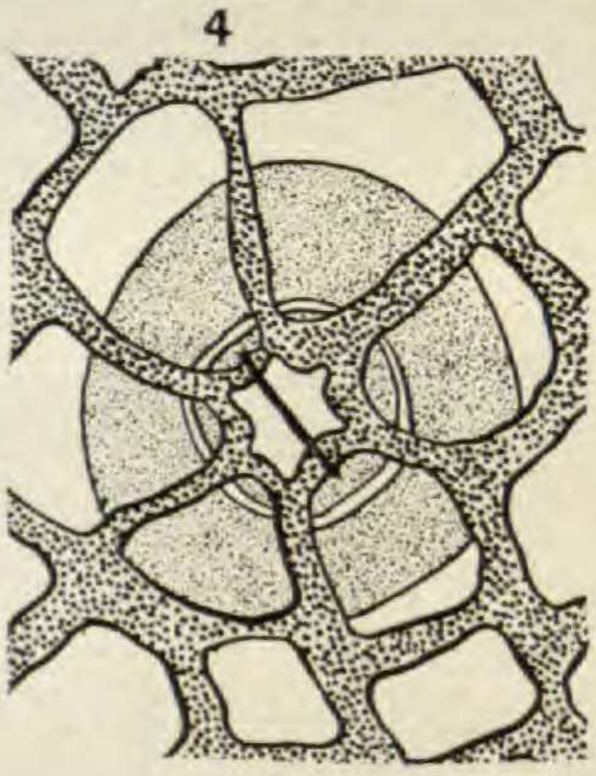

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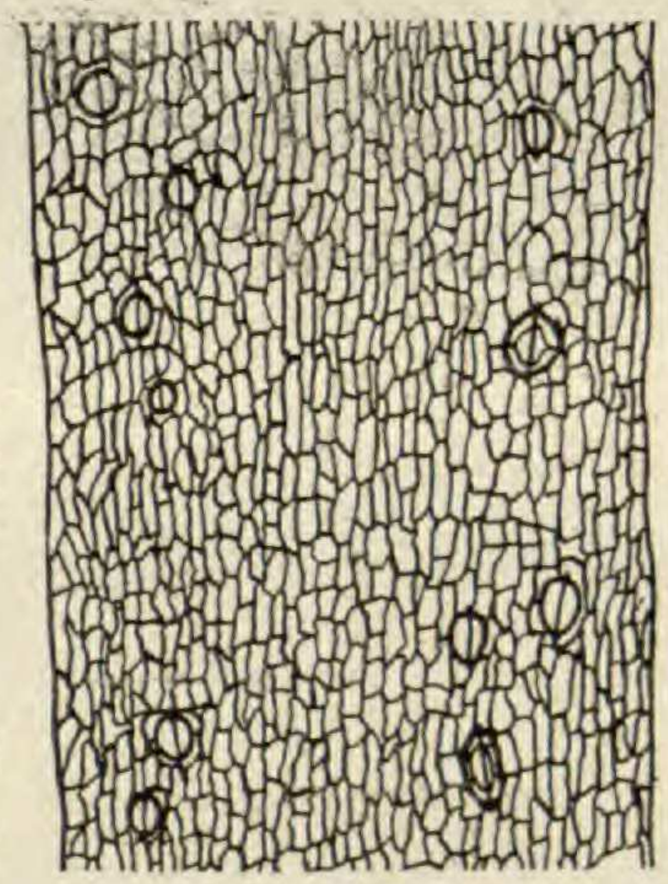

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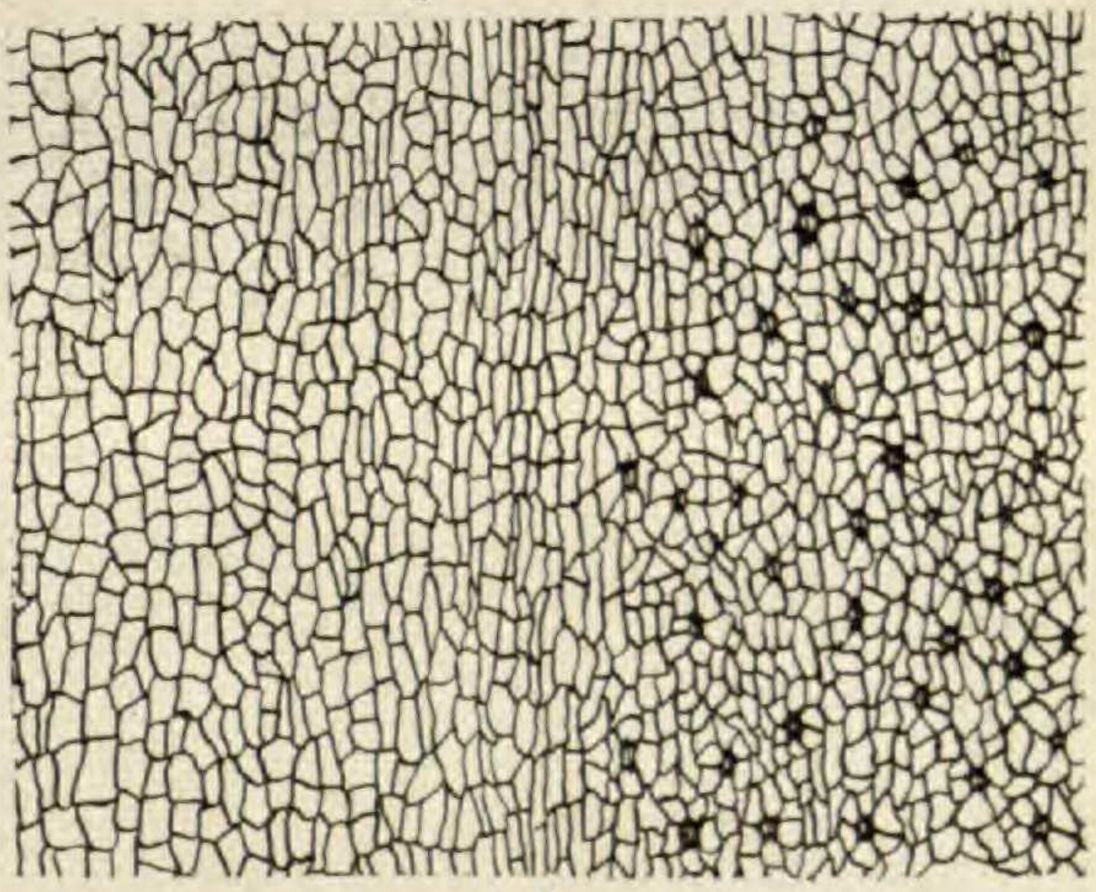

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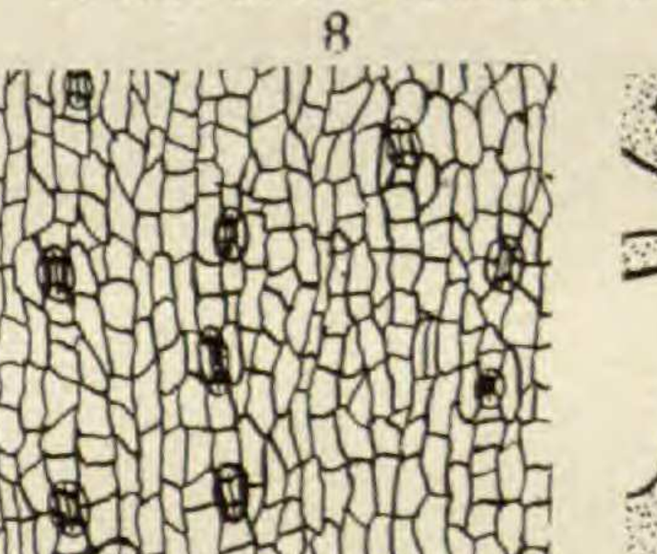

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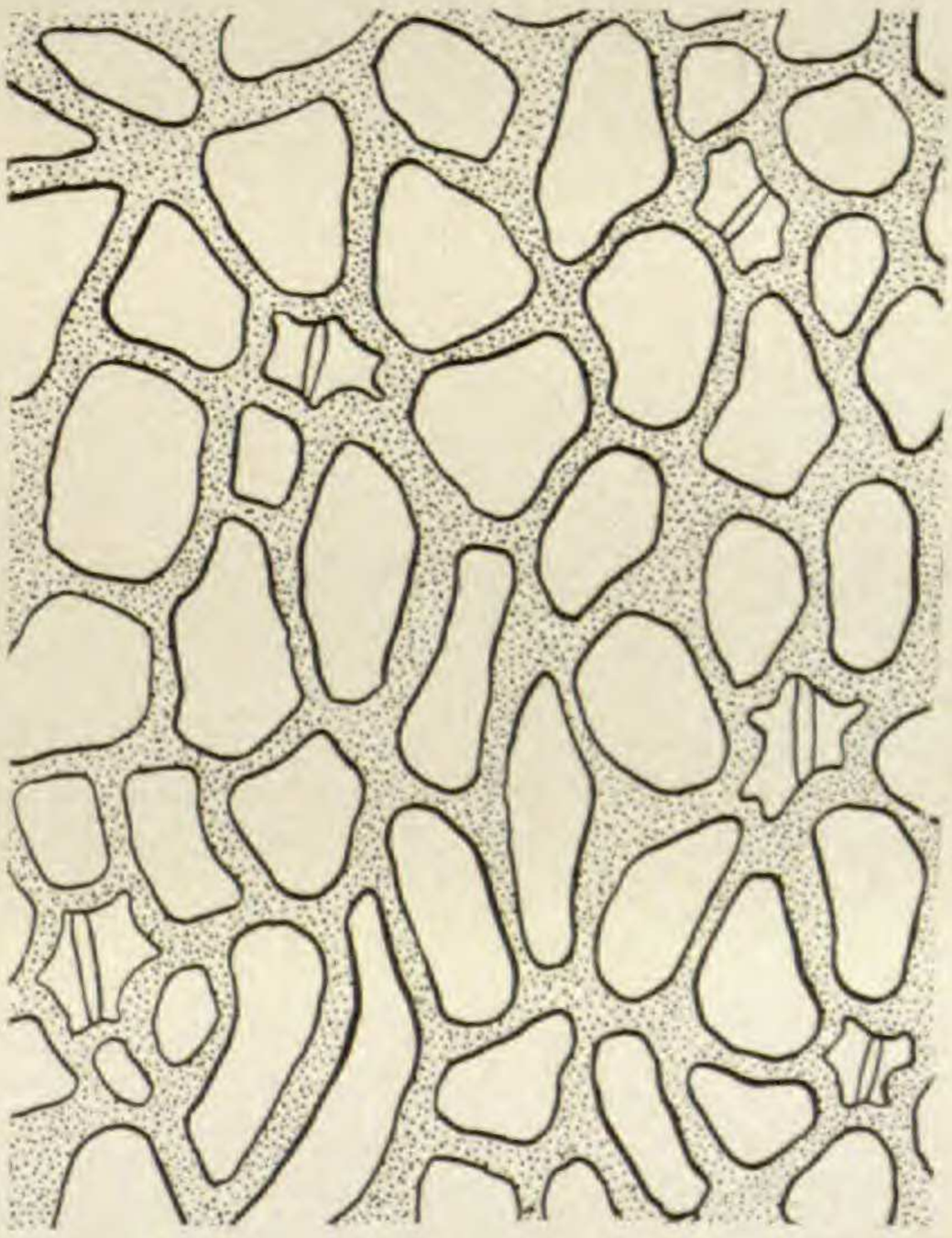

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HOLDEN on CONIFERS